SATPURA HYPOTHESIS AND THE DISTRIBUTION OF LAUGHING THRUSHES *GARRULAX* LESSON OF INDIA[1]

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(With two maps and a text-figure)

Several theories have been put forward to explain the discontinuous distribution of Himalayan flora and fauna in the south Indian hills. Tbe present paper discusses one of these theories in the light of an in-depth study of the ecology of Laughing Thrushes carried out between 1982 and 1984.

INTRODUCTION

The ecology of two south Indian endemic laughing thrushes, namely the Nilgiri Laughing Thrush *Garrulax cachinnans* and the Whitebreasted Laughing Thrush *G. jerdoni*, in the Nilgiri (11°12' N to 11°40' N and 76°14' E to 77° E) and Palni Hills (10°1' N to 10°26' N and 77°14' E to 77°52' E) was studied from May 1982 to mid March 1983 and July 1983 to August 1984. Three and a half months (20 March to 8 July 1983) were spent in the Nainital area, Uttar Pradesh, (29°12' N, 79°29' E) to learn the habitat, ecology and behaviour of laughing thrushes in their strong hold, i.e. the Himalayas, where most species of the genus *Garrulax* occur. In the Himalayas, four species of laughing thrushes were studied, namely the Streaked Laughing thrush *G. lineatus*, Whitethroated Laughing Thrush *G. albogularis*, Whitecrested Laughing Thrush *G. leucolophus* and the Striated Laughing Thrush *G. striatus*.

OBSERVATIONS AND DISCUSSION

Besides India, laughing thrushes occur in China, Pakistan, Nepal, Bhutan, Bangladesh, Burma, Thailand, Kampuchea, Malaysia and Sri Lanka (Map 1). The genus *Garrulax* comprises 46 species (Zuoxin 1982), of which 28 occur in the Indian subcontinent, mainly in the Himalayas. Of these 28 species, two are endemic: *G. cachinnans* to the Nilgiris and *G. jerdoni* to the Palnis and Kerala hills. The only other laughing thrush occurring in different south Indian hills is the Wynaad laughing thrush, which is a subspecies of the east Himalayan *G. delesserti* (Ali 1977). Only one species, *G. cinereifrons*, occurs in Sri Lanka as endemic, but it is closely related to *G. delesserti* (Ali and Ripley 1972).

The significant occurrence in a few hills of southern India of certain plant and animal forms either identical to or possessing close affinities with east Himalayan, Indochinese and Indo–Malayan forms, has been commented on by earlier biologists. Several theories have been put forward to explain this wide-ranging discontinuous distribution of life forms. Some of these are:

(1) Himalayan glaciation theory, (2) Southern route across the Indian ocean theory, (3) Deccan trap theory, (4) Continuous range theory, and (5) Satpura hypothesis.

The Satpura hypothesis was first postulated by Hora (1937a, 1937b) to account for the presence and distribution of torrential-river fishes of Malayan affinity in the Indian peninsular region, south of the Satpura-Vindhya-Assam Hills trend, in contrast to their supposed absence in the west Himalayan region. For more than 15 years his numerous scientific contributions (Hora 1938, 1949a, 1949b, 1950, 1951, 1952a, 1952b, 1953, 1955; Hora and Mathur 1952, Hora and Menon 1952, 1953) developed the original concepts. He synthesized geological, palaeobiogeographical, palaeontological, palaeobotanical, palaeoclimatological and meteorological evidence for a comprehensive theory governing

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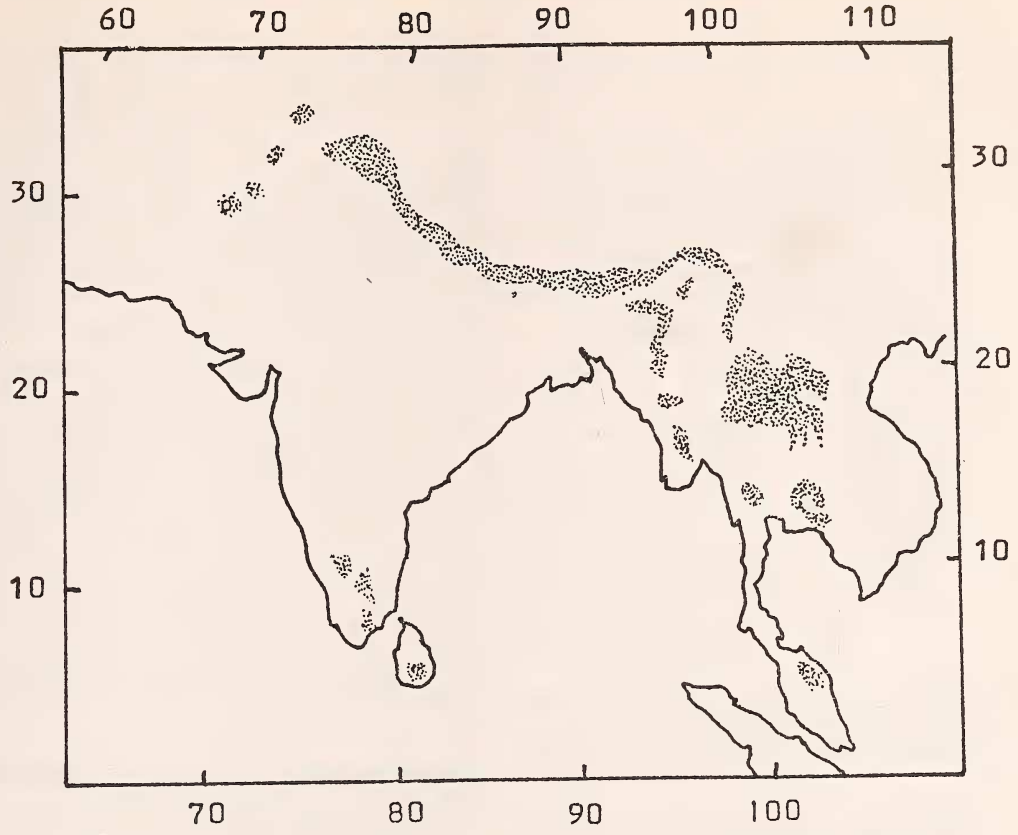


Map 1. Distribution of genus *Garrulax* (shaded portion only, modified after Ali 1953).

tertiary palaeobiogeography, faunal and floral migration and distribution.

Hora's (1937a) first statement on the hypothesis is paraphrased by Sahni (1982) as follows: The rising Himalayas in the region of western Assam and eastern Nepal disrupted the eastward flow of the Indo–Brahm river in the late Miocene which then acted as a barrier to a new stock of hillstream fishes migrating from the east towards India. Unable to cross the barrier, the fishes were deflected southwestwards along the Satpura—Vindhya trend which stretched across India as a pronounced range from Gujarat to the Assam Himalaya. The route followed by the fish immigrants was westward along the Satpura–Vindhya ranges, and thence southwards along the Western Ghats towards the southern extremity of the subcontinent (Fig. 1).

Ali (1949, 1977) supports Hora's Satpura Hypothesis and cites examples in the various groups of animals - mammals, birds, reptiles and amphibians. Ali mentions that many avian genera and species of the eastern Himalayas show a discontinuous distribution similar to that of the laughing thrush genus *Garrulax*, such as Fairy Bluebird *Irena puella*, Great Pied Hornbill *Buceros bicornis*, the two bazas or lizard hawks *Aviceda jerdoni* and *A. leuphotes* and the Rufous-bellied Hawk–Eagle *Hieraaetus kienerii*.

The most striking example among the avifauna is provided by the laughing thrushes of the genus *Garrulax*. Ali explains the origin of these relics, on the assumption that in the geological past there was a direct elevated land connection between the Himalayas and the southern hills, providing the requisite physiographical conditions for a con-

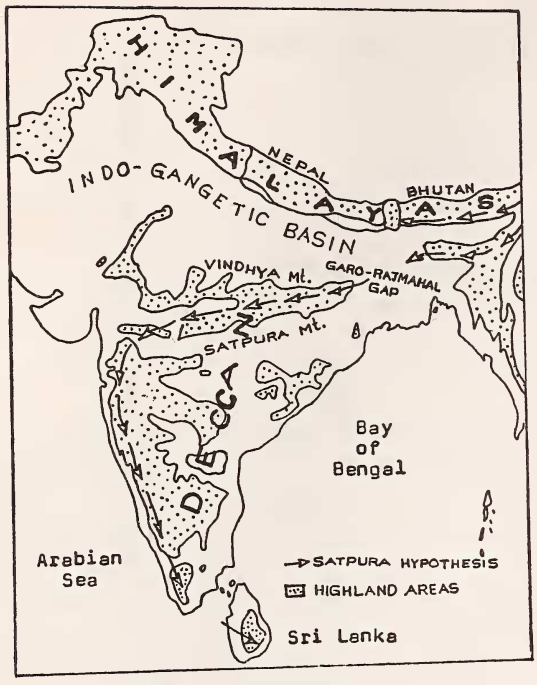
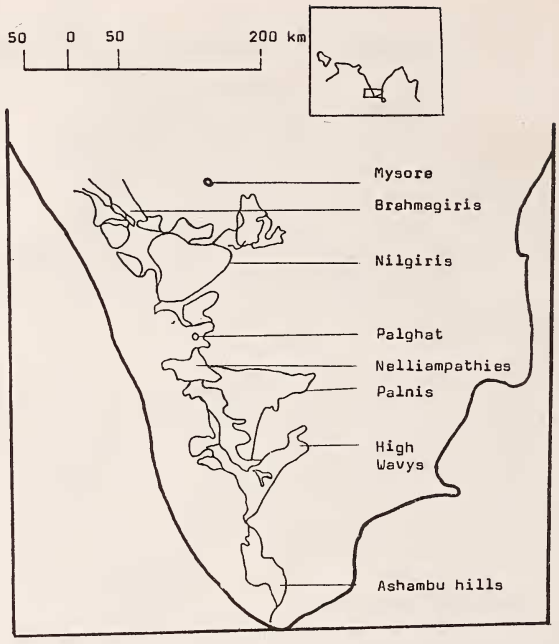


Fig.1 Sketch map of India illustrating Satpura Hypothesis of Hora. Arrows indicate the supposed migration routes of torrential river fishes (Source: Sahni 1982, modified after Hora 1953).



Map 2. Locations of the hilly areas of the Western Ghats (Source: Khan 1977).

tinuity in their distribution. Through the action of geotectonic forces–subsidence and erosion–the connecting land 'bridge' disappeared. The more stable sections were cut off from the Himalayas as 'islands' thus marooning the local populations of plants and animals on them, including weak–flying sedentary birds like the laughing thrushes, in a sort of natural refugium.

However, Dey (1949) asserts that it is impossible, on available evidence, to accept the idea of a belt of hills across the Bengal (Rajmahal) gap, Chota Nagpur etc. within the time— range of living animal species. Auden (1949) is also not in favour of the probability of the existence of the continuous Satpura ranges.

If, as suggested by Dey (1949) and Auden (1949), there was no continuous elevated land connection between the Himalayas and the south Indian hills, then the laughing thrushes could not have migrated southward over the Satpura-Vindhya mountains. On the other hand it would seem more likely for them to have spread over the continuous western Himalayas.

Moreover, the Satpura Hypothesis is unable to account for the following three facts regarding the present distribution and ecology of the southern laughing thrushes.

1. *G. cachinnans* is restricted to the Nilgiris, whereas *G. jerdoni* is found in the Brahmagiris, north of the Nilgiris, and Palnis, High Wavy and Ashambu hills, i.e. south of the Nilgiris. It is very unlikely that *G. jerdoni*, which is found in the Brahmagiris, completely by passed the Nilgiris on its passage towards the Ashambu hills (Map 2). If these birds had migrated through the Satpura-Vindhya mountain trend, the two endemic laughing thrushes *G. cachinnans* and *G. jerdoni* would have appeared together, at least in certain hills in the Western Ghats, particularly in the Nilgiris.

An in–depth study of the south Indian endemic laughing thrushes *G. cachinnans* and *G. jerdoni* has shown that both species have almost identical ecological requirements. Then the question arises as to what factors prevented these two endemic

species from coexisting in any of the Western Ghats hills in their range. Gause (1934) states that two species cannot coexist unless they are occupying two different niches.

Let us assume that due to identical niche preference these two species could not coexist. However, Perrins and Birkhead (1983) remark that closely related bird species often differ in one or more niche dimensions within a community. According to them the following might happen if two species with identical niches arrived in the same place: (1) They might coexist without deleterious effects. This is a possibility only if the resource is temporarily unlimited. (2) One or other species may be more efficient at harvesting a limited resource. In this case, either the less efficient species will become extinct, or it will change its niche. In cases where coexistence occurs it is unlikely that one species would change its niche completely and that the other would not change at all. It is more likely that each will be slightly more efficient than the other in different parts of the niche. If so, what would happen is that both species would alter their niches accordingly.

MacArthur (1972) points out that it is easier for two similar species to coexist than for three or more. This is because in the former situation each species has the chance of shifting its niche away from that of the other. With three or more species, this may not be possible for the species occupying the middle part of the resource. Furthermore, either each species maintains its niche and there is a considerable overlap between adjacent species, or each species narrows its niche. Hence, if the southern laughing thrushes had migrated through the Satpura–Vindhya trend, the coexistence of these two species would have appeared in some of the south Indian hills they inhabit. In the Himalayas several species of laughing thrushes do coexist.

2. The south Indian laughing thrushes are believed to be relict populations of Himalayan forms. Previous workers found the Himalayan species of the genus *Garrulax* to be chiefly group—living or gregarious birds. However, the present study reveals that the two endemic south Indian laughing thrushes are chiefly pair—living. If the south Indian populations are an offshoot of their group—living Himalayan congeners (author's experience of the Himalayan species is confined to the breeding season when *G. lineatus* and *G. striatus* were found only in pairs), the territorial strategy would have shown a different picture of their survival. Gaston (1980) states that an individual of a pair—territorial species can switch to group—territoriality without loss of fitness in terms of its pre—existing reproductive and feeding behaviour, but an individual of a group—territorial species which adopts a pair—territorial strategy may suffer in adaptations to feeding, predator detection and nest—site selection which reduces its fitness in a pair—territoriality. However, the nesting success of the southern endemic laughing thrushes appeared to be high which is an indication of how well they are adapted in their present distribution.

3. Furthermore, the complete absence of the Sri Lankan endemic laughing thrush, *G. cinereifrons* in the Western Ghats is again puzzling as it too would have migrated along the Satpura—Vindhya mountain trend. Although Jacob (1949) states that Sri Lanka remained geographically a part of the Indian mainland until quite recent times and supported Hora's Satpura Hypothesis, he admits that he has no direct geological evidence in support of the hypothesis to explain the existing distribution of the flora and fauna. Moreover, concerning the land connections between India and Sri Lanka, the common belief is that the last separation is as recent as *c.* 10,000 years ago, but the real disappearance of the Gulf of Mannar would, according to Blasco (1970), date from the commencement of the Pleistocene; and there is apparently nothing to prove that there was in its place a high mountain.

These unexplained facts do not fully credit Hora's concept (supported by Ali) of a physical corridor which enabled the southward migration of the laughing thrushes.

ACKNOWLEDGEMENTS

I am thankful to my professor the late Dr Salim

Ali for his guidance and keen interest at all stages of this work. I thank Mr J.C. Daniel, Curator, Bombay Natural History Society; Dr Ali Reza Khan, Assistant Professor, Department of Zoology, University of Dhaka; Dr Robert B. Grubh and Mr S.A. Hussain of the Bombay Natural History Society, who gave valuable advice during the course of this study. The study was supported by a fellowship grant from Salim Ali—Loke Wan Tho Ornithological Research Fund of the Bombay Natural History Society.

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